PAPER No. 353
UNIVERSITY OF CALIFORNIA
GRADUATE SCHOOL OF TROPICAL AGRICULTURE
AND CITRUS EXPERIMENT STATION
SUBTROPICAL, CALIFORNIA

UNIVERSITY OF CALIFORNIA
COLLEGE OF AGRICULTURE
AGRICULTURAL EXPERIMENT STATION
BERKELEY, CALIFORNIA

ENDOXEROSIS, OR INTERNAL DECLINE, OF LEMON FRUITS

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IMPERIAL MYCOLOGICAL INSTITUTE
9 DEC. 1937

BULLETIN 605
APRIL, 1937

UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA

CONTENTS

PAGE

Introduction ... 3
- Recognition of the problem ... 3
- Yearly fluctuations ... 3
- Distribution ... 3
- Age of trees and fruit ... 4

Symptoms ... 4
- Green fruit ... 5
- Silver fruit ... 5
- Yellow (tree-ripe) fruit ... 6
- General ... 6

Seasonal variation in different localities ... 7
Review of earlier reports ... 8
- Endoxerosis versus alternaria rot ... 9
- Tagging and measuring of young fruits ... 9
  - Growth rate ... 10
  - Water content ... 10
  - Acidity ... 11
- Withdrawal of water from fruits by leaves ... 11
- Potometer tests ... 13
- Gas conduction by sections of fruit twigs ... 14
- Gum formation in endoxerosis ... 14
  - Gum in the twig ... 14
  - Pith gumming ... 15
  - Gum in the lemon fruit ... 16
  - Pentoses and pentosans ... 18

Quantity of acid in healthy and endoxerotic fruits ... 19
Partial defoliation in relation to endoxerosis ... 20
Lemon trees in cheesecloth tents ... 20
- One tree in tent, grove *A* ... 21
- One tree in tent, grove *B* ... 21
- Two trees in nonventilated and ventilated tents, grove *B* ... 21

Bagging lemons ... 22
Oil-spray tests ... 22
Effects of irrigation practice ... 23
- Furrow versus overhead irrigation ... 23
- Application of different amounts of irrigation water ... 23

Strain and variety tests ... 27
Individual tree variation ... 28
Comparative amounts of endoxerosis on north and south sides of tree ... 28
Comparative number of seeds in healthy and endoxerotic fruits ... 28
Fertilizers in relation to endoxerosis ... 30
Discussion ... 31
Control measures ... 33
- In the grove ... 33
- In the packing-house ... 33

Summary ... 34
Acknowledgments ... 37
Literature cited ... 41

ENDOXEROSIS, OR INTERNAL DECLINE, OF LEMON FRUITS[1, 2]

E. T. BARTHOLOMEW[3]

INTRODUCTION

THE TERM "ENDOXEROSIS" (pronounced en-do-zer-ó-sis), which means "internal drying," is used to describe a physiological abnormality of lemon fruits. The disorder is characterized by the destruction of the internal tissues, especially in the stylar end of the fruit. The term "endoxerosis" is used here in place of the more common term, "internal decline," which was used during the earlier studies of the malady. "Blossom-end decay," "tip deterioration," "yellow tip," "pink tip," "dry tip," and similar terms have been used by growers, packers, and shippers in referring to this trouble in the past. When the study of endoxerosis was first begun, the terms just mentioned included such symptoms, now known as "membranous stain," as a browning of the "core" and of the membranes which cover the pulp segments of the fruit. The term "endoxerosis" applies here only to the abnormality having the characteristics mentioned in this paper.

Recognition of the Problem.—Endoxerosis has been recognized by the lemon growers in California for at least forty or fifty years. However, it was not considered a major problem in the industry until the supply of lemons produced approximated the quantity demanded for consumption, which necessitated restrictions upon the quality of the fruit shipped.

Yearly Fluctuations.—The seriousness of the endoxerosis problem fluctuates from year to year. For example, in some years as much as 60 per cent of the fruit of a given pick in some groves will have to be discarded or sent to the products plant on account of this trouble; in the same groves in other years, not over 10 to 20 per cent will have to be discarded. Climatic factors have an important bearing on such conditions.

Distribution.—Endoxerosis may be found, during the hot summer months, in almost any lemon grove in California. Groves situated within the hot inland valleys are especially likely to show comparatively large amounts of affected fruit. A great variation in distribution may occur not only with respect to different groves but also with respect to different

[1] Received for publication July 20, 1936.

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areas within a given grove. Some seasonal and locality variations are discussed on pages 7–8.

In addition to its prevalence in California, endoxerosis of lemons has been reported from Sicily[16] [4] and Australia.[13] It has also been reported from Palestine[15] in "citrus fruits" (orange, citron, and grapefruit), but the symptoms described do not agree with those for lemons in California. The symptoms reported from Sicily and Australia also differ somewhat, possibly owing to varietal and environmental conditions.

Age of Trees and Fruit.—Endoxerosis has been found in the fruit of trees of all ages, ranging from three or four years up to fifty years. Young, thrifty trees with heavy foliage as a rule show a much higher percentage of affected fruits than older ones with less dense foliage.

Endoxerosis does not usually affect the lemon fruit until it is practically mature.[5] The disorder may appear, however, in fruits that have been stunted and have not reached picking size. In some pickings, endoxerosis is found only in the yellow, tree-ripe fruits, but it often occurs also in the silver, light-green, and dark-green fruits from the same grove. The tree-ripe fruit usually shows the greatest percentage of the trouble.

SYMPTOMS

That cavities (lacunae) may form in fruits and in the vegetative tissues of certain plants when the water supply in these tissues is deficient, is a well-known fact. Such cavities, apparently caused by the withdrawal of excessive amounts of water from the fruits by the leaves, may be found in the peel of the stylar end of lemon fruits. The cells collapse and may be entirely destroyed, often being changed into such materials as pentoses and pentosans and eventually into gum.

The first cavities to appear in the lemon are adjacent to the vascular bundles. They mark the position of the canals which lead from the stigma down into the ovary. It is the cells lining the walls of these canals that are the first to collapse. Observations made after the cutting of many thousands of lemon fruits in this portion of the peel indicate that the formation of these cavities is the first evidence of desiccation and the first step in the production of endoxerosis. Experiments have shown that the amount of pentoses and pentosans begins to increase in this portion of the peel simultaneously with the formation of the cavities. The first visible evidence, after the formation of the cavities, is the exudation of a colorless gummy substance when the peel is cut in the stylar region.

[4] Superscript numbers in parentheses refer to "Literature Cited" at the end of the bulletin.

[5] The word "mature" as used here, and in the following pages, means that the fruit has attained picking size; it does not refer to the color of the fruit.

Green Fruit.—It is often impossible to determine without cutting whether or not a green fruit is affected. In some cases there is no external indication, except possibly a partial loss of luster at the stylar[6] end of the fruit. Many times a yellow or orange-yellow color may develop on the surface of a quarter or more of the stylar end, while the remainder of the fruit is still green; but even this condition is not a sure indication that the fruit is endoxerotic.

The first plainly visible internal symptoms are usually found in connection with the vascular bundles in the "nipple" of the peel at the stylar end of the fruit. The affected areas assume a pinkish to rust-brown color, and many of the vessels are clogged with gum. At this stage, the vessels and the surrounding tissues sometimes break down and form a mass of gum. In other cases the vessels are clogged with gum, but there is no noticeable breakdown of these or of surrounding tissues.

As endoxerosis progresses, pink to rust-brown splotches may appear in one or more places in the white inner portion (the albedo) of the peel on any part of the fruit. At this stage, the cells and juice sacs of the pulp at the stylar end of the fruit become affected, lose water, and collapse. In certain areas and at certain times of the year, the vessels all the way through the center of the fruit become discolored and filled with gum without seriously affecting other parts of the fruit. This is usually as far as the trouble has progressed in fruits that are picked while light or dark green.

Silver Fruit.—Endoxerosis is not easily detected by external signs at the silver stage of development of the fruit. In many cases a more intensive coloring of the peel at the stylar end of the fruit is an indication that the abnormal breaking down of the tissues has begun. But, as is often true of the green fruits, this indication may be misleading.

The loss of water and the collapse of pulp cells and juice sacs at the stylar end continue. The progress is more rapid near the center than out near the peel. It is especially rapid in the pithy core that runs through the center of the fruit. As the fleshy pulp tissues dry, they may retain their normal color, but more often they assume the characteristic pinkish or rust-brown color. In this stage the breaking down of the tissues has progressed until parts of the inner portion of the peel and perhaps a fifth of the adjoining pulp at the stylar end of the fruit have become affected.

[6] The "stylar" end of the citrus fruit is the free end, that which is opposite to the stem or attached end. In common usage the free end of the fruit is erroneously referred to as the "blossom" end. The petals (the conspicuous portion of the blossom) are attached at the base of the young fruit, which means that the blossom end and the stem end refer to the same portion of the mature fruit.

Yellow (Tree-ripe) Fruit.—With the yellow fruit also, the signs are far from infallible. The more intensive yellow or orange-yellow color which the stylar end takes on while the remainder of the fruit is still green persists after the fruit has become ripe, and in many instances serves as an indication of internal abnormality. If the peel of the lemon is comparatively thin, the breaking down and collapsing of some of the internal tissues in the stylar end of the pulp will cause the formation of a depression at the base of the nipple. In some cases the depression may appear on one side only, and thus cause the nipple to curve or bend over in that direction. However, this is not always a sure sign that the fruit is endoxerotic, since a similar condition may exist in healthy fruits, caused by the shrinking of the tissues in the peel directly beneath the nipple.

In the yellow fruit, there is little or no indication of a further breaking down of the cells in the peel, but the pulp tissues continue to lose water and collapse as long as the fruit remains on the tree. In general, when a third to a half of the pulp tissues at the stylar end have become affected, an abscission layer will form at the stem end, causing the fruit to drop from the tree.

General.—In all of the three classes of fruit just described, the external signs are such that perhaps 50 to 90 per cent of the affected fruits may be detected and culled out. Different lots vary greatly in this respect. In many instances, the trouble is not detected until the fruit is cut.

The breaking down of the tissues does not continue after the fruit has been picked. Tissues already affected may continue to lose water, collapse, and become discolored; but the trouble does not spread.

As more and more of the stylar-end pulp tissues become affected, that end of the fruit becomes lighter in weight than the stem end. For this reason, the badly affected fruits may be recognized and culled out at the time of washing because they, unlike the healthy ones, float with the affected end upward.

In the foregoing description of the symptoms of endoxerosis, a typical example has been cited. Endoxerosis may begin while the fruit is still green, or it may appear only in the silver or tree-ripe fruit. In the latter case, the gum formation and tissue discoloration may be less pronounced.

There are two other physiological maladies of lemon fruits which are not typical of endoxerosis but which, at times, may be associated with it and may be manifestations of the same trouble. One is a drying and collapse of the vesicles (juice sacs), principally in the stylar end of the fruit, without the discoloration or gum formation which accompany endoxerosis. The other is characterized by the formation of masses of gum in the "core" of the fruit, with little or none in the peel or pulp.

SEASONAL VARIATION IN DIFFERENT LOCALITIES

Reports concerning endoxerosis in southern California were received annually from 1926 to 1930 from the lemon packing-house inspectors of the California Fruit Growers' Exchange. The reports included such data as dates of first appearance of endoxerosis in different districts, amounts appearing over special periods during the summer, and the percentage of fruit affected during the entire summer. It is impossible to include here all of the interesting data obtained from the inspectors during this five-year period. Table 1 gives a portion of the data for the year 1929.

TABLE 1

PERCENTAGES OF ENDOXEROSIS IN YELLOWS, SILVERS, AND GREENS IN DIFFERENT SECTIONS OF SOUTHERN CALIFORNIA, APRIL TO NOVEMBER, 1929

Association	Dates	Per cent of endoxerosis, all colors
	Locality *A*	
1	June 10–Sept. 15	12
2	June 10–Sept. 15	10
3	June 15–Sept. 15	8
4	June 15–Oct. 1	15
5	June 15–Sept. 15	10
6	June 15–Sept. 15	10
7	June 15–Sept. 15	10
8	June 15–Oct. 1	8
9	June 15–Sept. 15	7
10	June 1–Oct. 1	10
11	June 15–Sept. 15	8
12	June 15–Sept. 15	6
13	June 20–Sept. 15	5
14	July 15–Sept. 15	Trace
	Locality *B*	
1	Sept. 1–Oct. 15	6
2	June 1–Oct. 15	6
3	Aug. 1–Oct. 15	2
4	June 1–Oct. 15	Trace
5	June 25–Oct. 17	8
6	Entire summer	Trace
7	Entire summer	Trace
8	Entire summer	Trace
9	Entire summer	Trace
	Locality *C*	
1	July 15–Sept. 1	1
2	July 1–Sept. 1	15
3	July 1–Sept. 1	12
4	July 1–Sept. 1	17
5	July 15–Sept. 1	7
6	July 1–Sept. 1	6
	Locality *D*	
1	July 1–Oct. 1	8
2	July 1–Nov. 1	5
3	July 1–Oct. 1	8
4	July 1–Nov. 1	3
5	July 1–Nov. 1	6
6	July 1–Oct. 1	5
7	July 1–Nov. 1	3
8	July 1–Oct. 1	5
9	July 1–Oct. 1	5
10	Entire summer	Trace
11	Entire summer	Trace
12	Entire summer	Trace
	Locality *E*	
1	June 1–Sept. 25	10
2	June 15–Oct. 15	6
3	June 15–Oct. 5	15
4	June 1–Oct. 5	20
5	Apr. 1–Aug. 15	5
6	May 15–Oct. 1	3

Table 1 shows that the total average amounts of endoxerosis appearing during the summer in different association packing-houses varied from a trace to as high as 20 per cent. The percentages given in the tables were based on a combination of actual tests and on estimates. The times when endoxerosis first appeared in appreciable amounts in the different packing-houses varied from April 1 in association 5, locality *E*, to August 1 in association 3, locality *B*. The dates at which it disappeared or became of minor importance varied from September 1 in all of the associations in locality *C* to November 1 in four of the associations in locality *D*. These dates give an idea of the differences in times of appearance and disappearance in different associations and in different sections of the lemon-growing areas of southern California.

Some of the other points of interest contained in table 1 and in other data from the inspectors' reports are as follows:

1. Climatic and other factors influence the time of the initial appearance of endoxerosis in a given year. This is indicated by the fact that in 1929 the disease was practically negligible until after the hot spell of June 19 to 21, whereas in 1930 it became of commercial importance from April 1 to May 15 in the different localities. During 1926 in one association, it began to appear as early as March.

2. Endoxerosis was much worse in some of the associations in a given locality than in others.

3. The dates on which the maximum amounts of endoxerosis appeared in a given association varied from year to year.

4. The maximum amounts of endoxerosis reported for a given pick in any association were 100 per cent of the yellows, 85 per cent of the silvers, and 60 per cent of the greens.

5. With the omission of those associations that have comparatively little endoxerosis, the reports showed that about 10 to 15 per cent of all the lemon fruits picked from May 1 to November 1 in southern California were endoxerotic.

REVIEW OF EARLIER REPORTS

Experimental studies on endoxerosis were begun in 1913 and have been continued more or less extensively ever since. The results of some of the tests which bear directly or indirectly on the subject of endoxerosis in California have been published elsewhere by Barrett,[8] Barrett and Fawcett,[9] Bartholomew, Barrett, and Fawcett,[6] Bartholomew,[1, 3, 4, 5] Bartholomew and Robbins,[7] and Fawcett and Lee.[10]

The following presentation includes some of the most important results obtained in the earlier work, along with the results of many later

tests which have never been published. For full details of the results obtained in the early investigations, the reader is referred to the publications indicated under the different headings.

ENDOXEROSIS VERSUS ALTERNARIA ROT

During the earlier studies of endoxerosis, a form of decay, now known as "alternaria rot,"[2] was considered by the growers and packers to be the advanced stages of endoxerosis.[7] At the present time the same notion persists, but to a much more limited extent. In 1920 and 1921, carefully conducted experiments with picked fruits were carried on in the laboratory and in many packing-houses. The results of these experiments showed that healthy fruits did not become affected with endoxerosis after they were removed from the tree and that those already affected with endoxerosis did not show increased development of the characteristic symptoms. Hundreds of tests showed that no fungus could be isolated from the interior of healthy or endoxerotic fruits tested as soon as they were brought to the packing-house or laboratory; yet the cultures showed that actual decay of the healthy and endoxerotic fruits after they had been kept in storage was caused in every case by a fungus. In almost every case *Alternaria* was the causal organism except, of course, where molds or other organisms had gained entrance through mechanical injuries due to handling. In a few cases such fungi as *Colletotrichum* and *Phomopsis* were the principal causes of the decay. The results of these experiments and extensive observations since that time indicate that the actual decay of the fruits is caused by a fungus and should not be attributed to the so-called "later stages" of endoxerosis.

TAGGING AND MEASURING OF YOUNG FRUITS

Young fruits were tagged and measured to determine the possible bearing on endoxerosis of: (1) the rate at which lemons increase in size, as influenced by climatic and seasonal changes, and by the time of year at which the fruit is set; and (2) the increase in acidity and water content of the fruits at different stages of their development.

The tests were conducted in three groves, six, twenty, and thirty years of age, respectively. Each grove was in a different lemon-growing district, but all three were of the Eureka variety. In each of the three groves, 200 small lemons were measured and tagged every month over a period of one year, and those that had been previously measured and tagged were remeasured. In this way each of a total of 5,600 lemons was meas-

[7] For a colored plate showing the characteristics of endoxerosis (internal decline), see Fawcett and Lee;[10] for one showing the differences in characteristics of endoxerosis and alternaria rot, see Bartholomew.[2]

ured every month until it dropped from the tree or until it came to maturity and was picked. The fruits chosen were on all different portions of the tree.

In testing the acidity (the strength of the acid), the fleshy pulp alone was used, but both peel and pulp were used in determining the water content. The fruits were cut once longitudinally and once transversely. One-half of each end was used for the acidity test and the other half to determine the water content.

Tests were also made to determine the comparative acidities of the stem and stylar halves of both healthy, mature fruits and of endoxerotic fruits, and the comparative amounts of acid in the stem and stylar halves of endoxerotic fruits.

Growth Rate.—The growth rates of the fruits were retarded during the colder parts of the winter and the hotter and drier parts of the summer. Also, the fruits set in late spring or early summer were more likely to be off-shape, rougher, and thicker-skinned than those set at any other time of the year. This was especially true of the fruits set on the older trees. In this grove, 60 to 70 per cent of the fruits set in late spring and early summer were off-shape, rough, or thick-skinned.

The growth rate of the individual lemon is influenced by soil and climatic conditions, by the time of year when set, and by the location on the tree. While the height on the tree and the location, whether within the foliage or exposed on the outside, appeared to have an influence, the most important factor seemed to be the condition of the branch on which the fruit was borne. The variation was probably due to differences in the amount of water and food or food materials carried by the different branches. For example, some of the fruits set in April were up to picking size in October and November, 7 and 8 months after being set, while other lemons on the same tree were not up to picking size for at least 14 months after being set. Such conditions appear to have an important bearing on endoxerosis, as will be explained subsequently in this paper.

Water Content.—The results of these tests showed that there is very little difference between the water content of the stem and stylar halves of the healthy lemon fruits, at least until they are mature. Their water content appears to be noticeably influenced by the availability of water and by transpiration. For example, in September, when the water supply was limited and transpiration relatively high, lemons approximately ¾ inch in diameter had an average water content of 54 per cent. In December, when both rain and irrigation water were available and the transpiration rate was low, the water content of lemons only ½ inch in diameter averaged 68 per cent.

Mature lemons may show considerable individual variation in water content. It increases comparatively slowly after the fruit has reached a transverse diameter of 1½ inches. Tests showed that lemons approximately 1½ inches in diameter had a water content of 83 per cent, and that those approximately 2¼ inches in diameter had a water content of 89 per cent.

Acidity.—The quantity of acid in a lemon increases until it reaches maturity and then decreases slightly,[1] but the acidity of the juice, like the water content of the fruit, increases comparatively little after the lemon has become approximately 1½ inches in diameter.

Variations in acidity were found not only in individual lemons but in the different ends of the same lemon. However, in over 400 mature, healthy lemons tested, the results, when averaged, showed practically no difference between the acidities of the stylar and the stem-end halves. When the average acidities of the stylar and stem halves of badly affected endoxerotic fruits were compared, differences were apparent, although they were not large.

WITHDRAWAL OF WATER FROM FRUITS BY LEAVES

Fruits which are turgid at night may become comparatively soft on a warm summer day, as is well known by citrus growers. When pruned branches are thrown on the ground and examined several hours later, the leaves on those branches which bear fruits are much more turgid than those on the branches which do not bear fruits. They also give a clue to one of the causes of endoxerosis. The following results, summarized from experiments reported earlier,[3] explain why this is true.

1. If a thin slice is cut from the stylar end of a lemon fruit which is still attached to a leafy branch and the cut end of the fruit is immersed in a dye, such as red ink, the dye will be drawn up into the leaves.

2. When branches are cut from a lemon tree and thrown on the ground, the leaves on those which do not bear fruits will wilt much more rapidly than on those which bear fruits. Such results are illustrated in figure 1. If some of the fruits are detached from the branches, those which remain attached will lose water about twelve to fifteen times as rapidly as those which have been detached. Results similar to the ones mentioned in this paragraph were obtained by Hodgson[12] while experimenting with the Washington Navel orange.

3. Lemon fruits about 1¾ inches in diameter, while attached to the leafy branches, were exposed to a temperature of 115° Fahrenheit (46° C) for 4½ hours. At the end of this period the sap concentration of these fruits was found to be 10.5 per cent greater than that of similar fruits

tested as soon as they were removed from the trees. That this difference was caused primarily by the withdrawal of water from the fruits by the leaves is shown by the fact that the sap of detached fruits exposed

Fig. 1.—Lemon fruits may act as reservoirs, supplying the leaves with water when they cannot get it from other sources. Photograph taken 48 hours after branches were cut from tree.

to the same conditions showed an increased concentration of only 1.5 per cent.

4. A special piece of apparatus, an auxograph, was constructed for the purpose of further studying the withdrawal of water from lemon fruits by the leaves.[3] The more important data obtained by the use of the auxograph may be summarized as follows: Other conditions being equal, the

greater the lapse of time after an irrigation, the greater the amount of water drawn from the fruits by the leaves each day. A normally growing lemon fruit may contract during the day and expand again at night, the degree of expansion exceeding that of contraction, so that the fruit slowly becomes larger from day to day. On the other hand, during periods of high temperature and low humidity, the contraction may exceed the expansion, so that the fruit may not only cease growing but actually become smaller. When soil moisture is low, this condition of fruit contraction may endure for as long as two or three weeks at a time. The change from contraction to expansion in the fruit may occur within 10 to 15 minutes. Such changes were recorded by the auxograph when a light shower occurred or when trees were sprayed with water during the middle of a summer day. During the long, dry summer days, if fog, dew, or clouds were not influencing factors, the fruits began to contract about 6 a.m. and continued to decrease in size until 5 to 6 p.m. During the winter months, the decrease in size began about 9 a.m. and continued until about 3 or 4 p.m. The maximum amount of water lost in a day (6 a.m. to 6 p.m.) by any one of the mature lemon fruits tested was about 5 cc.

POTOMETER TESTS

A check of the auxographic records made by the different lemon fruits during a certain series of tests showed that the endoxerotic fruits did not begin to contract as early in the morning and did not begin to expand as early in the afternoon as the healthy fruits. On an average, the endoxerotic fruits began to contract 1 hour and 25 minutes and to expand 1 hour and 10 minutes later than the healthy fruits on the same tree. It seemed that some condition within the fruits or in the twigs to which they were attached might be responsible for these results.

Potometer tests were made in order to obtain evidence on this point. Potometers are graduated glass cylinders. When they are properly attached to the ends of twigs from which the fruits have been removed, the comparative amounts of water absorbed and the rates of absorption by the different twigs can be determined. Many twigs on twelve different trees were used in this test. With one exception the twigs which had borne mature healthy fruits absorbed more water than those which had borne mature endoxerotic fruits. During the test period, the twigs that had borne the healthy fruits absorbed an average of 2.18 cc, and those that had borne the endoxerotic fruits absorbed only 1.28 cc, of water from the potometers. These results indicate that some condition in the twig (apparently in the water ducts), and not in the fruit, was at least largely responsible for the differences in the times of initial contraction

and expansion recorded by the auxographs for healthy and endoxerotic fruits.

The detailed records of this group of tests[4] show that approximately 94 per cent of the water withdrawn from the potometers by the twigs was withdrawn during the 14 hours from 5 a.m. to 7 p.m. In other words, nearly all of the water was withdrawn during the daylight hours.

GAS CONDUCTION BY SECTIONS OF FRUIT TWIGS

Twigs, similar to those which had been used in the potometer tests, were brought to the laboratory, where carbon dioxide was forced through them in order to obtain further data on their comparative conduction capacities.[4] Approximately 400 twigs or pieces of twigs were tested.

The results of these tests confirmed those obtained by the use of the potometers. One of the interesting additional results was that as successive portions of the tip ends of the twigs were removed, the amounts of gas that could be forced through the two kinds of twigs (those that had borne healthy and those that had borne endoxerotic fruits) became approximately equal. These results indicated that whatever it was that impeded the flow of water and gas was located in the twig not more than a few centimeters back of the point of the attachment of the fruit.

GUM FORMATION IN ENDOXEROSIS

The buttons and the first few centimeters of the tips of the twigs which had been used in the gas-conduction tests were kept for further study. Later they were cut into very thin transverse and longitudinal sections, stained, and studied under the microscope.[5] This study showed that many of the ducts in the buttons and in the tips of the twigs were partially or totally filled with gum. Similar studies showed that many of the ducts in the endoxerotic fruits were in the same condition. The following is a summary of the results of the study of gum formation in endoxerosis of lemons.

Gum in the Twig.—Gumming began in the stylar end of the fruit and advanced progressively into its basal end, then into the button, and finally into the twig itself. Therefore, the amount of gum, or whether any gum at all was formed in the twig that had borne an endoxerotic fruit, depended on the stage of gum formation in the fruit. In no case was gum of this type found in a twig that had borne a healthy fruit. That the gumming fruit was directly or indirectly responsible for the presence of gum in the twig was indicated by the fact that where a healthy and an endoxerotic fruit were borne side by side at the end of a twig, the branch of the twig (pedicel) directly back of the endoxerotic

fruit contained gum, whereas the one back of the healthy fruit did not (plate 1, *A*).

The presence and the location of gum in other portions of the twig are shown in plate 1, *B, C, D,* and *E*. An explanation of these figures may be found in the description accompanying the plate.

The distance that the gum extended back into the twig was governed by the extent of gum formation in the fruit; however, this distance seldom exceeded 2½ inches. By the time gumming had extended that far, the lemon had become so severely affected that an abscission layer had formed and the fruit had dropped. The formation of gum in the twig did not continue after the fruit had been removed. As in the case of the fruit, there was no external evidence that gum had formed in the twig. In all of the hundreds of twig segments examined, not one was found which showed gum in the bark or in the actively growing layer of tissue between the bark and the wood (the cambium).

The presence of gum in the ducts thus explains why the endoxerotic lemons began to contract and expand later than the healthy ones; why less water was drawn from the potometers by the twigs that had borne endoxerotic lemons; and why such twigs conducted less gas than the healthy ones.

Pith Gumming.—In this connection, another type of twig gumming is of interest. Growers often state that twigs having gum deposits in the pith are more likely to produce endoxerotic fruits than those which do not contain gum deposits. To the unaided eye, the deposits appear as more or less spherical, brownish areas in the pith. Microscopical examination showed that the cells of the affected tissue were usually intact and that the gum was both intra- and intercellular. In extreme cases, some of the cells were disintegrated and a gum pocket had formed. To determine any possible relation between these gum deposits in the twig and endoxerosis in the fruits, 1,782 twigs were split longitudinally and the comparative numbers of deposits determined. The twig lengths ranged from 6 to 18 inches. The results of these counts may be summarized as follows:

1. Gum deposits may be found in twigs less than a year old and even in suckers, but they are much more prevalent in twigs over one year old.

2. It was not uncommon to find as many as 10 to 15 gum deposits in a twig 1 foot long that had borne a healthy fruit, while a nearby twig bearing an endoxerotic fruit might contain only one or even no such deposits. In other cases, the conditions might be just the reverse. There was no consistent evidence that the presence of the deposits in the twigs was in any way related to endoxerosis in the fruits.

3. Gum deposits were slightly more prevalent in the twigs of the Eureka lemon than in those of the Lisbon, but there appeared to be no relation between this condition and the comparative amounts of endoxerosis in the two varieties.

4. Out of 200 twigs of each of the following varieties, there were 196 gum deposits in the twigs of the lemon, 4 in the Washington Navel orange, 2 in the Valencia, and 3 in the grapefruit.

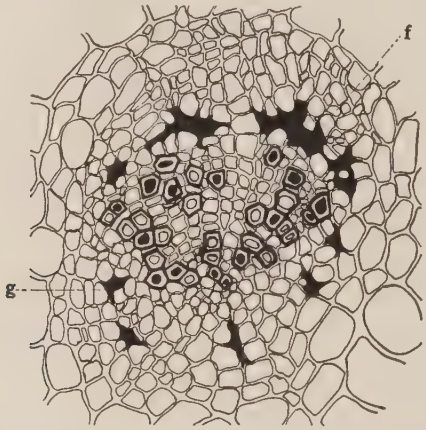


Fig. 2.—Cross section of a vascular bundle from a gumming area in the peel of an endoxerotic lemon fruit. Note gum formation in phloem at *f* and in bundle sheath at *g*. (Courtesy of the *American Journal of Botany*.)

5. There was no consistent difference in the number of gum deposits found in twigs taken from lemon trees in six plots, each of which had received a single different fertilizer for fifteen consecutive years.

6. A total of 52 twigs from six lemon trees of a variety that bore variegated leaves were examined. Of these, 26 bore only leaves of a light-yellow color. They appeared to be normal in every way except that they bore no visible green coloring matter. The other 26 twigs bore leaves that were variegated, that is, the leaves were partially green and partially light yellow. Only one very small gum deposit was found in the first lot of 26 twigs, while 21 of the second lot contained one or more gum deposits of the usual size in each twig.

Gum in the Lemon Fruit.—In perhaps the majority of cases, gum first becomes evident while the fruit is green in color, although sometimes it does not appear until after the fruit has become yellow. At first the gum is practically transparent, but soon the affected tissues and the accompanying gum assume the characteristic pinkish to straw-brown color.

The vascular bundles[8] in the peel of the stylar end of the lemon fruit are usually the places of origin of the first gum. From this point, its formation may extend into the central "core" of the fruit and to isolated areas in any portion of the white inner part of the peel. In the severer cases, gum may be formed in one-third to one-half of the pulp at the

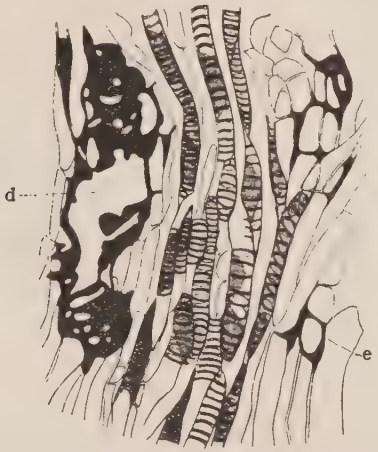


Fig. 3.—Longitudinal section of a vascular bundle from a gumming area in the peel of an endoxerotic lemon. Gum formation in the bundle sheath is shown at *e*, and the breaking down of the phloem at *d*. (Courtesy of the *American Journal of Botany*.)

stylar end of the fruit, with the result that the tissues collapse and eventually lose much of their water.

The tissues which are affected first are the phloem and the bundle sheath, especially the former; but the surrounding parenchyma cells may be affected a little later. A case in which the phloem has begun to form gum and to disintegrate is shown in figure 2, at *f*. A more advanced stage, in which the phloem is almost entirely disintegrated, is shown in figure 3, at *d*. The gum formation and disintegration of tissues may extend into the bundle sheath and progress until in places the xylem of the bundle may become entirely isolated from the surrounding tissues. In severe cases, where large gum pockets are formed, even the water-conducting vessels themselves become at least partially disintegrated, and segments of them may be found scattered promiscuously through the

[8] The "vascular bundle" is composed of the xylem, which contains the water-conducting vessels; the phloem, which transports such foods as the sugars; and the small cells surrounding the bundle, which are called the "bundle sheath." The larger cells which surround the bundle sheath are called the "parenchyma" cells.

gum masses. Figure 4, at *j*, *i*, and *h*, represents various stages of gum formation in the parenchyma cells, some distance from the vascular bundles.

As the gum is formed, it imbibes so much water that a pressure is produced. If a thin slice is cut from the peel of an actively gumming fruit, gum may be seen to exude almost instantly from the region of the affected vascular bundles.

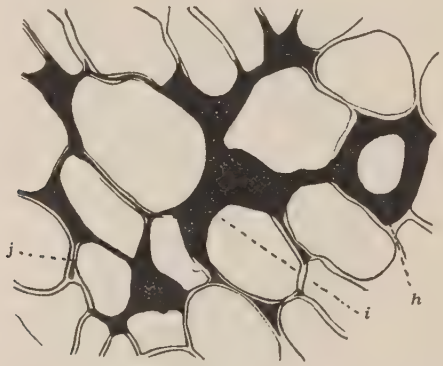


Fig. 4.—Section of a gumming area in the parenchyma of the peel of an endoxerotic lemon. Note the swelling between the walls of two adjacent cells at *j*, the disappearance of the wall on one side of the cell at *i*, and the complete disappearance of the wall of the cell at *h*. (Courtesy of the *American Journal of Botany*.)

Pentoses and Pentosans.[9]—Biochemical studies were made on the peels of healthy and endoxerotic lemon fruits in order to determine the comparative amounts of gum-forming substances in each.[10] In these tests,[7] the peel from one-fourth to one-third of the stylar end of mature or nearly mature healthy and endoxerotic lemons was used. The outer portion of the peel which bears the oil glands was removed. The remaining white portion was then cut into very small pieces, quickly dried to constant weight in vacuum, and ground to pass a 100-mesh sieve. The tests were made on the powder.

The results of these tests showed that a surprisingly large proportion of the peel of the fruits tested was composed of sugars or easily hydro-

[9] The pentoses are examples of some of the less common sugars, which are present in much greater abundance in some plants than in others. They are formed from the pentosans. The pentosans are products formed from the walls or contents of the cells. Gums and mucilages are formed from pentosans. Pectin contains much pentosan material.

[10] Credit is due W. J. Robbins of the University of Missouri for the major portion of this interesting piece of work, which is reported in greater detail in another paper.[7]

lyzable material. The amounts of hydrolyzable material were fairly constant, ranging from 25 to 35 per cent, whereas the sugars were more variable, ranging from 14 to 34 per cent. The pentosans, the materials from which gums may be formed, were from 39 to 63 per cent more abundant in the peel from endoxerotic fruits than in the peel from healthy fruits.

QUANTITY OF ACID IN HEALTHY AND ENDOXEROTIC FRUITS

While the changes which occur in the fruit during the development of endoxerosis do not materially lower the strength of the acid which remains in the tissues,[1] they do materially decrease the total amount of the acid. In order to determine the extent of the latter, 20 tree-ripe endoxerotic lemons were halved transversely and the juice reamed from the stylar and stem halves separately. The quantity of juice obtained from the stylar (endoxerotic) halves was 385 cc, and that obtained from the stem halves was 525 cc. The total acid in each of these two quantities, in terms of anhydrous citric acid, was equivalent to 16.4 cc in the stylar and 27.6 cc in the stem halves.

The next tests of this nature were made on whole, tree-ripe healthy and endoxerotic lemons. The amount of juice that could be reamed from 80 endoxerotic lemons was 2,874 cc and from the healthy fruits 3,754 cc. Titration tests showed that the endoxerotic fruits contained only 73.7 per cent as much acid as the healthy fruits. These results show plainly that such lemons as these are not suitable for market purposes. These lemons had been kept in storage for some time, and the fact that they were endoxerotic was not known until some of them were cut just before being packed for shipment. The fact that they had been in storage in this condition explains why the acid content was only 4.50 to 5.25 per cent, whereas that of the average healthy lemon runs from 6 to 7 per cent.

The results of the tests show that there may be considerably less juice and acid in yellow, and sometimes in silver, endoxerotic lemons than in healthy ones. Often, however, the endoxerotic condition in the fruits has not progressed far enough to cause an appreciable decrease in the amount of juice or acid. This is especially true of the light- and dark-green lemons in which the affected tissues are confined mostly to the tissues of the peel. Such lemons might be placed on the market as far as decrease in juice or acid content is concerned. However, their vitality has become weakened, and as a result they are more susceptible to the attack of such fungi as *Alternaria*.

PARTIAL DEFOLIATION IN RELATION TO ENDOXEROSIS

It was thought that excessive foliage transpiration might be a factor in producing endoxerosis in lemon fruits. In order to test this possibility, approximately one-half of the leaves were removed from three trees in each of two groves in different districts in 1921. The trees in these two groves were six and eight years old, respectively. The picking was according to ring size (2.25 inches), and each fruit picked was cut to determine the percentage of endoxerosis in the total pick. The test trees

TABLE 2

EFFECT OF PARTIAL DEFOLIATION ON GROWTH RATE OF YOUNG LEMON FRUITS

Date	From nondefoliated trees		From partially defoliated trees	
	Number of lemons	Average diameter* of fruits	Number of lemons	Average diameter* of fruits
July 29	100	20.8	100	19.3
August 26	96	37.1	86	34.3
October 4	93	50.0	84	45.6
Total increase	..	29.2	..	26.3

* Expressed in thirty-seconds of an inch.

were partially defoliated in July and the picking tests were made in August, September, and October.

The partially defoliated trees in the six-year-old grove produced 3 per cent endoxerosis, and the controls produced 13 per cent. In the eight-year-old grove, the partially defoliated trees produced 6 per cent endoxerosis and the controls produced 16 per cent. The partial defoliation did not prevent endoxerosis, but the controlling effect was apparent.

However, partial defoliation should not be used as a control measure because of its retarding effect upon the growth rate of the fruits. The extent of this effect is shown in table 2. Although the retarding effect on growth (about $\frac{3}{32}$ of an inch) was not so great as might be expected, no doubt the effect was persistent and expressed itself in the tree behavior over a considerable period of time.

LEMON TREES IN CHEESECLOTH TENTS

In order to obtain further evidence as to whether reduced transpiration might be a factor in decreasing the amount of endoxerosis, cheesecloth tents were placed over certain trees during two different summers. In the first test (1922), two trees, one in each of two groves (groves *A* and *B*), were completely enclosed in the cheesecloth tents.

In a second test (1924), two trees in grove *B* were enclosed in a non-

ventilated tent and two other trees in a well-ventilated tent. The latter was done to keep the direct rays of the sun from striking the trees and at the same time to permit better air movement than in the closed tent. Comparative transpiration rates, both inside and outside of the tents, were determined by using porous, white atmometer spheres. Thermographs and maximum and minimum thermometers were also kept in standard shelters inside and outside of the tents. Comparative relative humidities were determined by using a sling psychrometer. The trees were enclosed about the middle of May and the tents removed the latter part of November. Fruit pickings were made at intervals between those two dates. A 2.25-inch ring was used in picking, but all fruits that had turned yellow before reaching ring size were picked each time.

One Tree in Tent, Grove A.—During the period from May to October, the fruit from one of the covered trees in the first test showed 0.01 per cent endoxerosis, whereas the fruit on the two adjacent trees showed 10.44 per cent.

One Tree in Tent, Grove B.—During the same period, the fruits on the other covered tree in this test did not show any endoxerosis, whereas the fruit on the two adjacent trees showed 28.40 per cent.

Two Trees in Nonventilated and Ventilated Tents, Grove B.—From May to October, 2.56 per cent of the fruit from the trees in the nonventilated tent showed endoxerosis, those in the ventilated tent showed 12.88 per cent, and eight adjacent trees showed 15.35 per cent.

The results of these tests indicate that the reduction of the rate and amount of transpiration from the trees had a marked controlling effect upon the amount of endoxerosis in the fruit. It is not surprising that more endoxerosis should develop in the nonventilated tent containing two trees than in those containing only one tree; for the former was considerably larger. The atmometer in the small tent lost 47 per cent and the one in the large tent lost 59 per cent as much as the atmometer outside.

Although there was not very much difference between the amounts of endoxerosis on the trees in the ventilated tent and on the control trees, the following fact is of interest: On September 12, the picking date on which more than three-fourths of the endoxerosis for the season was found, 66 per cent of the silvers in the controls and only 50 per cent of the silvers in the ventilated tent were endoxerotic. The amount of endoxerosis in the ventilated tent was 76 per cent of that of the controls, and the evaporation loss from the atmometer in this tent was 72 per cent of that of the one outside. These results indicate that water loss by transpiration is a more important factor in producing endoxerosis than are the direct rays of the sun.

The season's record showed that 100 per cent of the fruits in the small tents, but only 42 per cent in the controls, were up to ring size at time of picking. (At each picking all colored fruit was removed regardless of whether it was up to ring size.) The average for the season also showed 1 per cent yellow, 25 per cent silver, and 74 per cent green fruit from the tent, as compared with 12 per cent yellow, 75 per cent silver, and 13 per cent green fruit from the controls.

Temperature readings inside and outside of the tents were taken with tested maximum and minimum thermometers from July 23 to August 12. There was not over 1° Fahrenheit difference between the maximum temperatures. The minimum temperatures were 2.8° higher in the closed and 1.4° higher in the ventilated tent than outside.

From June 6 to August 9, relative-humidity readings, taken with a sling psychrometer, were made at about 2 o'clock each afternoon. The relative humidity in the ventilated tent was often the same and never more than 2 per cent greater than that outside, while the relative humidity for the nonventilated tent ranged from 2 to 6 per cent greater than that outside. These data refer only to the tents containing two trees each. The results indicate that wind movement noticeably increases the transpirational loss from the trees.

BAGGING LEMON FRUITS

During the early part of the study of endoxerosis (August, 1926), 500 lemon fruits about one-half to two-thirds ring size in the Station grove were covered with Manila bags. Three months later the bags were removed, and the comparative numbers of these and neighboring fruits that were affected with endoxerosis were determined. The presence of the bags neither augmented nor reduced the number of fruits affected. These results indicate that the direct rays of the sun and the reduction of transpiration from the surface of the fruits are not important factors in the production of endoxerosis.

OIL-SPRAY TESTS

Tests were made to determine whether or not oil sprays would reduce transpiration enough to produce a controlling effect upon the amount of endoxerosis in the fruit. Thirteen trees in grove *A* and twelve in grove *B* were sprayed with a 1¾ per cent oil emulsion in May, 1923. In May, 1924, twenty-five and twelve trees, respectively, in the same groves were sprayed with a 2½ per cent oil emulsion. The trees sprayed in 1924 were not the ones that had been sprayed in 1923. An equal number of adjacent trees served as controls.

The results of these tests indicate that the oil sprays applied did not have a consistent controlling effect upon endoxerosis. In the June pick, which was the first one after application of the spray, there seems to have been a controlling effect, except in grove *B* in 1924, when the difference was negligible. Much the same results occurred in the picks of September, 1923, and August, 1924, except in grove *B*, where there was considerably more endoxerosis on the sprayed trees than on the controls. These two picks are mentioned because they showed higher percentages of endoxerosis than any of the other picks for the two seasons. However, the averages, with the exception of grove *B* in 1923, show that there was practically no difference in the amounts of endoxerosis on the sprayed and on the control trees; perhaps a trace more was found on the sprayed trees. The June pick showed the greatest controlling effect. This is to be expected because tests have shown that while oil sprays reduce transpiration for a time, as the season advances the transpiration rate of the sprayed trees increases, and other conditions being comparable, may even surpass its rate before the oil spray was applied. While the number of trees used in the tests was comparatively small, the results at least indicate that it would not be advisable, aside from other effects that the oil may have on the trees, to attempt to control endoxerosis in a commercial way by spraying the trees with oil emulsions.

EFFECTS OF IRRIGATION PRACTICE

Furrow versus Overhead Irrigation.—In the summers of 1925 and 1926, tests were made to determine whether the method of irrigation would influence the amount of endoxerosis in the fruit. In grove *A*, a plot of trees was irrigated by means of an overhead sprinkling system, and an adjacent plot by the usual furrow system. There were two intervening rows between the test plots. The same plan was followed in grove *B*. The results of those tests are shown in table 3.

The results of the irrigation tests show that in each case the trees that were irrigated by the sprinkler system produced the least endoxerosis. The differences, however, are small, and it is doubtful whether they are significant. The expense of installing a sprinkler system for the purpose of controlling endoxerosis would certainly not be justifiable.

Application of Different Amounts of Irrigation Water.—An experiment to determine the effect of applying different amounts of irrigation water has given very important information concerning the cause of endoxerosis. Twelve Eureka lemon trees, budded on sour-orange stock, were used in the experiment. Buds for the scions were taken from a single parent tree of known origin. The sour-orange seedling stocks were

all grown from seed from one parent tree. The stocks were selected for uniformity of type, size, and vigor before budding was done. In the same manner, the twelve budlings to be used were later selected from a comparatively large number of budlings. They grew in the nursery for two years before being planted in lysimeter tanks.

The twelve cylindrical tanks in which the trees were planted were 10.0 feet in diameter, 4.0 feet at the edge, and 4.5 feet deep in the center. There was a drainage outlet in the center of the bottom of each tank.

TABLE 3

EFFECTS OF FURROW AND OVERHEAD-SPRINKLER IRRIGATION ON THE PRODUCTION OF ENDOXEROSIS

Date	Grove	Number of fruits cut	Per cent endoxerotic	
			Furrow irrigated	Overhead sprinkler
1925	A	2,550	36	32
1925	B	2,561	26	22
1926	A	1,983	33	27
1926	B	2,215	13	10

The tanks were filled with mixed, screened, virgin, top soil, the same amount from each wagonload of soil being placed in each tank. This was done to insure uniformity of soil composition for all tanks. The soil type was Ramona sandy loam. The soil was allowed to settle in the tanks during the winter before the trees were planted. The tanks were buried in the ground to within about 3 or 4 inches of their rims.

Figure 5 shows one of the twelve trees growing in the lysimeter tanks, three years after it was planted. The trees at this time averaged over 10½ feet in height. The production of the trees was good during the course of the experiment, the fruit yield equaling or exceeding field production in many localities. This photograph was taken before reservoirs were placed adjacent to each tree.

The trees were planted in May, 1927, and all received the same treatment until June, 1931. In May, 1931, they were divided into three groups of four trees each. By this time the trees had been producing fruit for two and one-half years. The grouping was based on the total amount of endoxerotic fruit produced by each tree from the time of initial bearing (January, 1929) to June, 1931.

The application of different amounts of irrigation water to the trees in the tanks began in June, 1931, and continued until the experiment was terminated on December 31, 1934. Water was applied to the soil in each tank when its total soil mass had reached an average moisture con-

tent of 6 to 8 per cent in group 1, 5 to 6 per cent in group 2, and 4 to 5 per cent in group 3. Water was measured in and applied from a reservoir that stood adjacent to each tree. The amount of water to be applied was determined by standard methods of soil-moisture determination. Holes left in the soil by the soil tube were filled with screened top soil

Fig. 5.—One of the twelve trees grown in lysimeter tanks. The trees were three years old and averaged over 10½ feet in height when this photograph was taken.

similar to that originally placed in the tanks. Water was applied in a spiral trench that began near the edge of the tank and ended within about 1 foot of the tree trunk.

Rainfall was measured in a rain gauge that stood near the experimental group of trees and was taken into consideration in applying irrigation water.

Before differential water treatment was begun, the apparent specific gravity, moisture equivalent, and wilting coefficient of the soil at each foot level in each tank were determined. The apparent specific gravity of the soil in all tanks was found to be 1.5. Moisture-equivalent values

clustered around 11 per cent as a mean with only very small deviations. Wilting-point values all fell within the range of 3.5 to 4.0 per cent. As a result of these findings, the values 11 per cent and 4 per cent were adopted as the standard moisture equivalent and wilting point, respectively, for the soil in each tank.

Most of the fruit was picked according to the regular ring-size method, but windfall, tree-ripe, sunburned, and endoxerotic fruits which did not attain full ring size were included as a part of the tree yield. The total

TABLE 4

PROPORTIONS OF GOOD AND ENDOXEROTIC FRUIT PRODUCED BY TREE GROUPS 1, 2, AND 3 FROM 1929 TO 1934, INCLUSIVE

Group	1929–1931			1932–1934				
	Condition of fruit			Soil moisture content*	Irrigation water applied†	Condition of fruit		
	Good	Endoxerotic				Good	Endoxerotic	
	pounds	*pounds*	*per cent*	*per cent*	*gallons*	*pounds*	*pounds*	*per cent*
1	1,389	137	9	6–8	47,677	1,984	245	11
2	1,219	151	11	5–6	44,920	1,895	211	10
3	1,414	106	7	4–5	38,545	1,604	328	17

* The figures in this column indicate the amount of moisture in the soil each time when irrigation water was applied during the period 1932–1934. For the period 1929–1931, all trees received like amounts of water.

† Differential water treatments were begun in June, 1931.

yield and the endoxerotic fruit produced on each tree were weighed at each picking.

The principal results obtained in this experiment are shown in table 4. The data in the table show that before differential water treatments were begun, the fruit yields of groups 1 and 3 were practically the same, whereas group 2 produced somewhat less than the other two. Although the total production of good fruit over the entire period from 1929 to 1934 was greatest for group 1, the increase in yield during the second period (period of differential water treatment) over that of the first period was greatest for group 2. The increases in the production of good fruit for the second period over those of the first period were 575, 676, and 190 pounds, respectively, for groups 1, 2, and 3. The increases in yields of endoxerotic fruit for the second period were, respectively, 108, 60, and 222 pounds.

Table 4 shows that during the period over which all groups received equal amounts of water, group 2 produced the greatest percentage of endoxerotic fruits and group 3 the least. During the second period (1932–1934), group 2 produced practically the same percentage of

affected fruits as during the first period (1929–1931); there was a slight increase in group 1 and a comparatively marked increase in group 3.

A single pick on August 6, 1934, after several days of hot weather, showed results similar to those shown in table 4, but even more marked. In this pick, 561 fruits from group-1 trees, 459 from group-2 trees, and 1,915 from group-3 trees were endoxerotic. In other words, group 1 produced 29 per cent and group 2 only 24 per cent as many endoxerotic fruits as were produced by group 3, the group receiving the least amount of water. The trees in group 3 did not suffer because of lack of soil moisture during this period of stress; they had received an irrigation just prior to the beginning of the hot spell. The 1,915 endoxerotic fruits from group 3 represented 62 per cent of the pick from that group.

It is of interest also that the sizes of the endoxerotic fruits for the period 1932–1934 were smaller for group 3 than for either of the other two groups.

TABLE 5

Comparative Susceptibilities of Different Strains of Lemons to the Production of Endoxerosis

Variety	Strain	Per cent endoxerosis	
		1925	1926
Eureka	Small open	41	22
	Eureka	29	25
Lisbon	Open	46	50
	Lisbon (dense)	40	42

STRAIN AND VARIETY TESTS

Tests were made during the summers of 1925 and 1926 to determine whether any difference could be found in the susceptibilities of different strains and varieties of lemons toward the production of endoxerosis.[11] All of the fruit of each picking during the two summers was cut to determine the percentage of endoxerosis produced on the selected trees of each strain. The results of these tests are shown in table 5.

Although the data in table 5 are limited and cover a period of only two summers, they show that the Lisbon strains in this case produced more endoxerosis than the Eureka strains. Some of the growers and packing-house men report similar conditions. However, the reports from

[11] These tests were made through the coöperation of A. D. Shamel and C. S. Pomeroy of the United States Department of Agriculture in one of their bud-selection plots.

others are just the reverse, so that in general there is probably very little difference in the susceptibilities of the two varieties.

The data do not show any marked difference in susceptibility between strains within a given variety.

INDIVIDUAL TREE VARIATION

Tests were made to determine whether a given tree that had produced more endoxerosis than an adjacent tree one year would continue to do so from year to year.

Some fruit trees that produce physiologically abnormal fruits are more or less constant in the amounts of such fruit that they produce each year; that is, if a tree produces more abnormal fruits than the adjacent trees in a given year, it does the same during the succeeding years. The fruit from forty-one Eureka lemon trees was examined over a period of four successive years to determine whether this condition applies to the production of endoxerosis.

A few of the trees showed a fairly marked constancy toward a low and others toward a high production of endoxerotic fruits. While it is true that some of the trees, over the four-year period, never produced as much endoxerosis as some of the other trees, there was such a marked fluctuation in the amounts produced by the majority of the trees that constancy would appear to be an exception rather than the rule.

COMPARATIVE AMOUNTS OF ENDOXEROSIS ON NORTH AND SOUTH SIDES OF TREE

Specific tests to determine comparative amounts of endoxerosis on various parts of the tree were conducted for two consecutive seasons in one grove each in three different counties; minor tests and observations were made in other groves over a longer period of time. The results of these tests showed that as a rule more endoxerosis appears on the south than on the north side of the tree. This is especially true for young trees, fifteen years of age or under.

COMPARATIVE NUMBER OF SEEDS IN HEALTHY AND ENDOXEROTIC FRUITS

The number of developed and undeveloped seeds in different lots of lemon fruits from five packing-houses were counted in order to determine whether fertilization and the development of seeds in a lemon fruit might have a bearing on its vitality and hence its susceptibility to endoxerosis.

The results of these tests are shown in table 6. The general averages in the table show that there were fewer developed and undeveloped seeds in the endoxerotic fruits than in the healthy ones. However, in some cases, there were more of either developed or undeveloped seeds in the

TABLE 6

Comparative Numbers of Developed and Undeveloped Seeds in Healthy and Endoxerotic Lemon Fruits

Source of fruits	Number of fruits	Total number of seeds per lot of fruit		Average number of seeds per fruit	
		Developed	Undeveloped	Developed	Undeveloped
Healthy fruits					
A	40	74	77	1.85	1.92
B	72	353	193	4.90	2.68
C	33	32	192	0.97	5.82
D	55	130	53	2.36	0.96
E	48	39	20	0.81	0.42
Total and average	248	126	107	2.18	2.36
Endoxerotic fruits					
A	40	23	18	0.58	0.45
B	60	309	146	5.15	2.45
C	33	52	164	1.58	4.97
D	54	65	50	1.20	0.93
E	30	29	12	0.97	0.40
Total and average	217	96	78	1.90	1.84

endoxerotic than in the healthy fruits. Twenty-five per cent of all healthy and 20 per cent of all endoxerotic fruits examined contained no seeds, either developed or undeveloped; 15 per cent of all healthy and 15 per cent of all endoxerotic fruits contained developed seeds only; and 14 per cent of all healthy and 12 per cent of all endoxerotic fruits contained undeveloped seeds only. Although the numbers of lemon fruits involved in the counts were not especially large, it seems fairly safe to conclude that the number of seeds, either developed or undeveloped, in a lemon fruit is not an important factor with regard to endoxerosis. From these results, it would appear that the keeping of bees in a grove to aid in pollination, with the resultant increase in number of seeds per fruit, would not necessarily decrease the percentage of endoxerosis.

Other data obtained during the study of this problem showed that the number of seeds per fruit varied with the season and with the conditions at the time of pollination and fruit setting.

FERTILIZERS IN RELATION TO ENDOXEROSIS

Efforts were made to determine what effect, if any, different fertilizer treatments may have on the prevalence of endoxerosis. Ammonium sulfate was applied to three plots in a grove near San Dimas in 1926 as follows: 5 pounds per tree to plot *A* in March; 5 pounds per tree to plot *B* in March and in May; and 10 pounds per tree to plot *C* in March and in May. Plot *D* (check plot) received no fertilizer. Three pickings were made from July to September and the fruit examined for endoxerosis. There was as much difference between the amounts of endoxerosis produced by individual trees within a given plot as there was between the total amounts produced by the different plots. There was really a slight increase in the amount of endoxerosis from the trees in each of the three fertilized plots over that of the check plot, but the differences were not large enough to be of significance. The same plots, without the application of additional fertilizer, showed no appreciable distinguishing effects of the ammonium sulfate on the production of endoxerosis during the following summer.

At the same time that the ammonium sulfate test was made at San Dimas, a similar opportunity was had for testing fruit from a block of trees in a grove near Riverside. In this plot dried blood was the source of nitrogen. The blood was applied at the rate of 16 pounds per tree. An adjacent plot of similar size and in the same grove, without blood, served as a check. During the two following summers there was only 1 per cent difference in the amounts of endoxerosis from the two plots.

Some growers have expressed the opinion that there is less endoxerosis in those groves in which the soil contains an abundant supply of available phosphates than in those in which the supply is average or below. Although no specific tests were made in this line, the results of tests made in the Rubidoux fertilizer plots at Riverside did not confirm this opinion. There was no appreciable difference in the amounts of endoxerosis from the plots that had received ample applications of phosphate for fifteen consecutive years and from those that had received no phosphate. Of course, it is understood that these findings and those mentioned in the two preceding paragraphs apply only to the location and conditions under which these tests were made.

The results mentioned in the first two paragraphs of this section were confirmed by tests made in the Rubidoux fertilizer plots. It may be said also that none of the many other fertilizers used on the Rubidoux plots appeared to have any appreciable effect upon the amount of endoxerosis produced by the trees. The Rubidoux fertilizer plots were located at the

University of California Experiment Station at Riverside. Blood, manure, potash, phosphate, and many other fertilizers were used. These fertilizer tests were begun in 1907 and were terminated in 1932. Cuttings to determine the percentages of endoxerosis on these plots were made in 1925 and 1926.

DISCUSSION

The formation of endoxerosis in lemon fruits is apparently not caused by any one factor in the fruit, in the tree, or in the environment. The creation of daily and protracted water deficits in the fruits during the warm summer months, as indicated by the auxograph, appears to be the most important contributing factor. This conclusion is substantiated by the results obtained: (1) when transpiration was reduced by covering the trees with the tents, (2) by partial defoliation, (3) by the presence of desiccation cavities in the stylar end of the fruits, and (4) by the results of the differential water treatments.

A further indication that a water deficit in the fruits may be a factor in causing endoxerosis is that gum forms first in the proximity of the water-conducting vessels in the stylar end of the fruit, which is the farthest from the source of water supply. In this connection, Klotz and Haas[14] have found that the sugar content and osmotic value are lower for the peel of the stylar end than for the stem end of the lemon fruit. Therefore water can be withdrawn most easily from these tissues.

In the twig, the gum forms first in the vessels nearest to the pith. These vessels are the least active in water conduction and thus are the most subject to desiccation. Higgins[11] found that a water deficit in the tissues very decidedly stimulated gum formation. The lack of water in the fruits cannot be the only factor, however, because the dry winds of the fall of the year cause a greater water deficit in the fruits than exists at any other time of the year, yet comparatively little endoxerosis is caused by this deficit.

Under the usual field conditions, heat also appears to be a very important factor. This conclusion is confirmed by the fact that endoxerosis is much more abundant in the interior districts than in those near the coast, and by the fact that it develops in the fruit only during the warm months of the year, principally during excessively hot spells. In these cases, heat is being considered as a direct factor and not in its relation to transpiration rates. Higgins,[11] in working with such twigs as peach, plum, and cherry, found that relatively high temperatures were the most likely to cause gum formation.

A temperature of 90° to 100° F and a relative humidity of 20 to 25 per cent in June are much more likely to cause the production of endoxer-

osis than a temperature of 100° to 110° F and a relatively humidity of 15 to 20 per cent in September. From this it appears that high temperature is not the only factor concerned. This is further borne out by the fact that the trees in the lysimeter tanks were all subjected to the same temperatures, yet some produced much more endoxerosis than others; the trees in the closed cheesecloth tents and the controls were subjected to practically the same temperatures, yet those in the tents produced practically no endoxerosis, while the controls produced comparatively large amounts; again, the partially defoliated trees produced less endoxerosis than the controls, yet both were exposed to the same temperatures.

The amount of water that is lost by transpiration through the surface of the fruit is of minor importance in the production of endoxerosis as compared with that which is withdrawn from the fruit by the transpiring leaves.

The nature and balance of the chemical substances, as well as temperature and water relations in the tissues, may be important factors in determining whether or not endoxerotic conditions will be manifested in the fruits when the periods of stress come. This may explain why endoxerosis is most prevalent during that portion of the year in which growth activities are greatest. It is a well-established fact that young, actively growing trees, as a rule, produce the largest percentage of endoxerotic fruits. These factors may also help to explain why the trees in the lysimeter tanks that received the greatest amount of water produced a slightly larger percentage of endoxerosis than those which received a moderate amount. Swarbrick,[17] in working with such trees as the plum and apple, found that gum formation in wounded tissues was decidedly more rapid and abundant during the period when growth and sap movement were most active than at any other time of the year. In this connection, it should be noted that endoxerosis is always worse after a series of winters of scanty rainfall. This condition would affect the growth reactions of the trees and also might well have a direct bearing on the subject of water relations.

The different phases of the problem of endoxerosis which have just been discussed show that the problem is an intricate one. That it can be solved in a commercial way, with the present varieties of lemons in use, appears unlikely. It may be possible, however, to find or develop an otherwise suitable variety or strain that will be less susceptible to endoxerosis.

CONTROL MEASURES

In the Grove.—Endoxerosis in lemon fruits appears to be a malady which is impossible to avoid or even to control to any great extent in a commercial way. A good tree root system and the proper amount of moisture in the soil have been found to be alleviating factors, but to determine just what is the "proper" amount of water for the many different types of soil on which the trees are grown is a difficult problem.

Reducing temperature and leaf transpiration and increasing relative humidity have also proved effective in decreasing the amount of endoxerosis, but commercially these methods are prohibitive because of the cost.

Freezing temperatures should be avoided if possible. Such a shock weakens the tree and the fruit and causes the formation of substances which may be more easily converted into gum and may eventually result in the desiccation of the fruit tissues.

Perhaps the surest and most economical means of obtaining partial control of endoxerosis is to use a smaller picking ring during the warm spring and summer months than during the remainder of the year. Fruits whose growth has been checked during warm weather because of insufficient moisture are especially susceptible to endoxerosis when they begin to grow again. Slow-growing fruits are usually much more susceptible, and rapid-growing fruits appear to be somewhat more susceptible, than fruits which grow at a moderate rate. It follows then that anything that can be done to prevent such conditions will decrease the amount of endoxerosis.

As a rule much endoxerosis may be avoided if all colored fruit is removed from the trees in early spring even though it has not attained the regular ring size. Climatic conditions in the spring and the amount of rain during the preceding months should govern the time of making the cleanup pick. It should be made early after winters of minimum rainfall or when hot spells come early in the spring.

The use of a comparatively small picking ring or the decrease in length of interval between picks is not only good insurance against endoxerosis, but it also means that the fruit, because of its greater vitality, will have a better storage and shipping quality.

In the Packing-House.—In the packing-house, detection of endoxerotic lemons without cutting them is difficult, although in the majority of cases, endoxerosis can be detected by determining its characteristics in a given lot of fruit. The characteristics may vary in different lots, but they usually consist of lack of luster or overcoloring of the stylar end of the fruit, sunken nipples, or the floating with the stylar end up of badly

affected fruits. Fruits should be cut as each new lot comes on to the grading belt in order to make sure that the supposed characteristics are reliable. For the sake of the reputation of the better brands of fruit, it is better for the graders to overcull rather than undercull in cases of doubt.

SUMMARY

A description of the characteristics of endoxerosis, varieties affected, general distribution, the differences between endoxerosis, alternaria rot, membranous stain, and other similar data are given.

Desiccation cavities adjacent to the vascular bundles in the peel of the stylar end of the fruit were the first indications that endoxerosis had begun to develop in the fruit; a detailed description of subsequent symptoms is given.

The lemon inspectors' reports showed that the maximum amount of endoxerosis in a given pick in any association was 100 per cent of the yellows, 85 per cent of the silvers, and 60 per cent of the greens. These reports also showed that, omitting the districts in which there is very little endoxerosis, approximately 10 to 15 per cent of the fruit picked from May 1 to November 1 in southern California was endoxerotic.

Lemon fruits that grow either slowly or very rapidly were found to be more susceptible to endoxerosis than those which grow at an intermediate rate.

The strength of the acid in endoxerotic fruits was practically as great as that in healthy fruits, but the amount was reduced in proportion to the injury.

Partial defoliation of the trees resulted in a decrease of endoxerosis during the immediately succeeding summer months.

Trees covered with cheesecloth tents produced no or only a trace of endoxerosis, whereas the controls produced comparatively large amounts.

Reducing transpiration by spraying the trees with oil was not found to be a practicable means of controlling endoxerosis.

Different tests showed that comparatively large amounts of water may be withdrawn from the fruits by the transpiring leaves. Marked water deficits were found to exist in the fruits for periods ranging from a few hours to two weeks, or even longer.

Auxographic records showed that during the long, dry summer days, provided that fog, dew, or clouds were not influencing factors, the lemon fruits began to contract, owing to the withdrawal of water, about 6 a.m. and continued to decrease in size until 5 to 6 p.m. During the winter months the decrease in size began about 9 a.m. and continued until 4 to 5 p.m.

Endoxerotic fruits began to contract later in the morning and to expand later in the evening than healthy ones.

Twigs that had borne endoxerotic fruits withdrew an average of only a little over one-half as much water from the potometers as did those which had borne healthy ones.

There was considerable variation in the amounts of gas that could be forced through twigs that had borne endoxerotic fruits, but the amounts were less than could be forced through twigs that had borne healthy fruits.

As gum formation proceeded in the fruit, the cells collapsed and the tissues became desiccated to the extent that badly affected fruits could be detected in the washer, the affected fruits floating higher and usually with the stylar end upward.

The gum in the fruit appeared to be formed largely from the cell-wall components and that in the twig principally from the cell contents.

The pentosans, the material from which the gum was formed, were from 39 to 63 per cent more abundant in the peel from endoxerotic fruits than in the peel from healthy fruits.

The first visible indication of endoxerotic gumming appeared in the region of the vascular bundles in the peel of the stylar end of the lemon fruit. Gum formation progressed toward the stem end in both peel and pulp. In the later stages, gum formed in the woody portions of the pedicel and adjacent twig. The gum in the vessels of the fruit prevented the ready entrance and exit of water, as indicated by the auxograph. The gum in the vessels of the pedicel and twig governed the rate at which they drew water from the potometers.

The examination of 1,782 twigs showed that the prevalence or absence of gum deposits in the pith had no bearing on whether or not the fruits would become endoxerotic.

Less endoxerosis was formed where the trees were irrigated by the overhead sprinklers than by the furrow method, but the differences were too small to warrant the recommendation of the former method as a means of control.

In a controlled test in which the lemon trees were grown in large tanks, those trees which had received the minimum amount of water produced much more endoxerosis than those receiving the medium amount; on the other hand, trees receiving the maximum amount produced slightly more affected fruits than those receiving the medium amount. For example, in a single pick, after an especially hot spell, 561 of the fruits from the trees receiving the maximum amount of water, 459 from those receiving the medium amount, and 1,915 from those receiving the minimum

amount, were endoxerotic. Also, the total amount of fruit produced by those trees which received the medium amount of water was considerably greater than by those which received the minimum amount and slightly greater than by those which received the maximum amount.

There appeared to be no consistent difference between the amounts of endoxerosis produced by the two standard varieties of lemon, the Eureka and Lisbon, nor between strains within either of these varieties.

The data presented indicate in a general way that some trees within a given grove may produce much and others comparatively little endoxerosis over a period of years, but exceptions to this are numerous.

The time of the first serious outbreak of endoxerosis in a given spring or summer depends largely upon the rainfall of the previous winter and the time of appearance of the first hot spell. The time varies from year to year.

More endoxerosis appeared on the south than on the north side of the trees, especially on young trees.

Lemon fruits set at certain times of the year and under certain conditions produce more seeds than those set at other times of the year and under other conditions. The conditions governing the number of developed or undeveloped seeds in a lemon fruit do not appear to be a factor in determining whether it will become endoxerotic.

Bagging of lemon fruits did not appear to have any effect on whether or not they would become endoxerotic.

No consistent or marked evidence was obtained that showed that different fertilizers may affect the amount of endoxerosis produced by the trees.

In general, the results of the numerous experimental tests indicate that daily and protracted water deficits in the tissues concerned, high temperatures during the actively growing season, and the presence of substances which are more or less readily convertible into gum are the most important factors in producing endoxerosis in lemon fruits.

The data presented substantiate other accumulated evidence that the members of the genus *Citrus* are strongly inclined to produce gum in their tissues when subjected to adverse conditions.

Certain control or alleviating measures for grove and packing-house practice are suggested.

ACKNOWLEDGMENTS

Grateful acknowledgment is made for the interest and helpful suggestions offered by J. T. Barrett and H. S. Fawcett during the earlier part of this study, and to E. C. Raby for assistance during the latter part; to H. W. Nixon and the other lemon inspectors, the packing-house managers and foremen, and to many growers, all of whom so willingly gave their coöperation; to the Lemon Men's Club for financial aid during a part of this study; and to A. D. Shamel and C. S. Pomeroy, of the United States Department of Agriculture, for their assistance in executing one portion of the work.

PLATE 1

A, Longitudinal section of a lemon twig that had borne a healthy and an endoxerotic fruit on adjacent pedicels; the healthy fruit at *h* and the endoxerotic one at *e*. Note gum in vessels of twig of *e* and none in vessels of *h*.

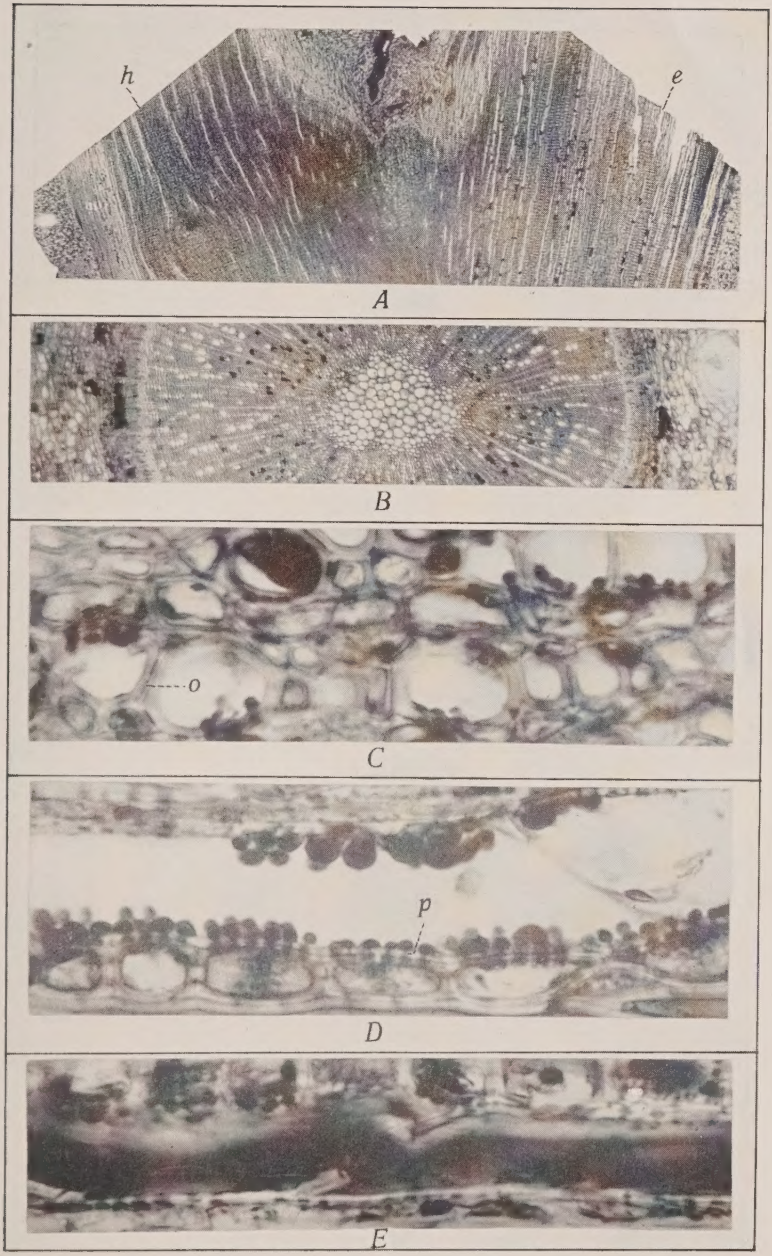
B, Cross section of a lemon twig that had borne an endoxerotic fruit. Many of the vessels are plugged with gum. The twig was probably not over ten months old; the annular appearance in the woody zone is due to different growth cycles during that period.

C, A portion of the cross section illustrated in *B* but more highly magnified. Note abnormal condition of cell walls at such places as are indicated by *o*.

D, Portion of a single water-conducting vessel and adjacent cells as seen in a longitudinal section of a pedicel that had borne an endoxerotic fruit. Note migration of gum through the pores, as indicated at *p*, and similar places.

E, Similar to *D*, except that in this case the vessel has become completely filled with gum.

(Courtesy of the *American Journal of Botany*)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